

A review of the biology of the Southern Bell Frog *Litoria raniformis* (Anura: Hylidae)

Graham H. Pyke

Frog Ecology and Behaviour Group Australian Museum
6 College St. Sydney NSW 2000

Email: grahamp@austmus.gov.au

ABSTRACT

The Southern Bell Frog *Litoria raniformis*, like the closely-related Green and Golden Bell Frog *Litoria aurea*, is considered to be threatened with extinction and subject to the future development of strategies aimed at its recovery. A necessary component of this recovery process will be a detailed and comprehensive review of available biological information concerning this species. This paper aims to provide such a review.

Litoria raniformis is, at least in comparison with *L. aurea*, poorly studied and many aspects of its biology warrant further investigation. Research conducted to date, however, reveals few, if any, differences in biology between the two species. They are similar in size, appearance, call, breeding biology, habitat and general behaviour.

Recovery strategies for the two species are therefore likely to be similar. Both are apparently threatened by habitat loss and modification, and by predation by the introduced Plague Minnow or Gambusia *Gambusia holbrooki*, and so may benefit from increased legal protection and control of Gambusia impact. Both are able to live in sites that are largely or completely human-made, and so may benefit from programs to either enhance or develop suitable habitat. Disturbance, either natural or human-induced, is apparently important to both frog species.

Key words: *Litoria raniformis*, threatened frog species, *Gambusia holbrooki*, frog conservation

Introduction

The Southern Bell Frog *Litoria raniformis* is, like a number of other Australian frog species, considered to be threatened with extinction throughout its range, though its official designation varies with geographic and political region. At a National level it is listed as 'vulnerable' under the Commonwealth *Environmental Protection and Biodiversity Conservation Act 1999* and 'vulnerable' in the *Action Plan for Australian Frogs* (Tyler 1997). At a State level it is listed as 'endangered' under the New South Wales *Threatened Species Conservation Act 1995* and in *Threatened Frogs of New South Wales* (Ehmann and White 1997), as 'vulnerable' under the Victorian *Flora and Fauna Guarantee Act 1988*, and as 'vulnerable' under the Tasmanian *Threatened Species Protection Act 1992*.

Given this 'threatened' status under both Commonwealth and State legislation, 'recovery plans' or 'action statements' are required for *L. raniformis* in all political regions where it occurs, where these 'plans' or 'statements' are expected

to contain strategies whereby the risk of extinction for the species can be decreased. However, no such 'plans' or 'statement' have so far been produced.

A pre-requisite for the development of a 'recovery plan' for any threatened species is a review of available information concerning the biology of the species (Pyke and White 2001; Pyke and Read 2001). Yet no such review exists for *L. raniformis*.

My aims were therefore to

1. Review all available information with regard to the biology of *L. raniformis*, identifying what is known as well as what is not known about the species;
2. Consider implications of this review in terms of recovery and/or management of the species;
3. Consider the nature and extent of further research on *L. raniformis* that could benefit the recovery process for this species and/or our understanding of its biology.

This review was developed using the strategy recommended in Pyke (2000). I divide it into sections based on the level at which observations regarding the species are focussed (i.e., species, individual, population, biological community), how these observations are made, and issues such as conservation and management of the species. Within each of these sections there are also sub-sections that reflect what is known about this species.

Biological review: *Litoria raniformis* (Keferstein 1867)

A. Species level

Identification

Litoria raniformis is known by a number of different common names including Green Tree Frog (Pickard and Towns 1988), Growling Grass Frog (Hero *et al.* 1991), Warty Frog (Robinson 1993), Warty Swamp Frog (Bennett 1997; Tyler 1997), Golden Frog (Waite 1928), Green and Golden Frog (Martin and Littlejohn 1982), Golden Bell Frog (Spencer 1888) and Southern Bell Frog (Ehmann and White 1997; Tyler 1992, 1997). Southern Bell Frog is the most widely used of these names.

It is a large frog, generally brownish-green or greenish-brown above and off-white below, with a lateral stripe running the length of the body (see Tyler 1978; Martin and Littlejohn 1982; Hero *et al.* 1991; Cogger 2000 for descriptions). It has numerous wart-like bumps on the side of the body below the lateral line and some above the line. The back has irregular areas of green and brown with the green ranging from a dull olive to a bright emerald-green and the brown ranging from a dull dark brown to a bright gold (Martin and Littlejohn 1982; Hero *et al.* 1991). There is usually a continuous narrow pale-green band running down the middle of the back and the area around the groin and backs of upper thighs is usually bluish-green to blue in colour (Tyler 1978; Martin and Littlejohn 1982). Adults reach up to about 90-100 mm (Barker and Grigg 1977; Bell 1982a, b).

The dorsal pattern varies considerably from one individual to another (Bell 1982a; Ashworth 1998) and may vary with both season and local conditions. Individuals that are sheltering under some object may become dark brown in dorsal colour, but are able to quickly become considerably lighter and brighter in colouration upon exposure to sunlight (Bell 1982b; Hoser 1989). Individuals may also tend to become darker in appearance during the non-breeding season (Waite 1928).

The morphology of *L. raniformis* seems well suited to its general habit of living either on the ground or in the water, rather than being arboreal (Waite 1928; Tyler 1978). It has a streamlined head, muscular hind legs and extensively webbed toes, all of which make it a powerful swimmer (Waite 1928; Cree 1985). It also has relatively small toe pads as befits its generally ground-level life (Waite 1928; Barker and Grigg 1977; Tyler 1978; Cree 1985).

Males of *L. raniformis* have a distinctive mating call which consists of a long growl or drone, either followed or preceded by a few short grunts (Waite 1928; Littlejohn 1963; Barker and Grigg 1977; Bell 1982b; Martin and Littlejohn 1982; Gill 1986; Hoser 1989; Osborne 1990; Hero *et al.* 1991). Spectral analysis of this call reveals a unimodal distribution of sound frequencies that range from about 900 to 1700 Hz and peak at about 1200 Hz (Loftus-Hills 1973). It is similar to the calls given by other members of the *Litoria aurea* species group (Osborne 1990; Thomson *et al.* 1996; see below). Examples of calls of the members of this group can be heard on several commercially-available tapes and cds (e.g., Stewart 1998).

A study of responses of midbrain auditory neurones of *L. raniformis* to sounds of different frequencies found the greatest sensitivity was to frequencies similar to those that make up the mating call (Loftus-Hills 1973). In this regard this species is similar to a number of other frog species (Loftus-Hills 1973).

Adult males can be distinguished from females on the basis of 'nuptial pads' or 'rugosities' on the first digit or 'thumbs' of their front limbs (Waite 1928; Martin and Littlejohn 1982; Ashworth 1998). These pads are recognisably distinct from the rest of the digit as raised areas that vary from a very dark brown during the breeding season to a pale colour similar to that of the rest of the digit during the remainder of the year (Ashworth 1998). Adult males also generally have darkly mottled throats while females have relatively clear off-white throats (Ashworth 1998).

Eggs are very similar to those of other members of the *Litoria aurea* species group but recognisably different from other co-occurring frog species (Pyke pers. obs.). Eggs are laid in a gelatinous matrix as floating mats that soon break up and sink to the bottom or loosely adhere to underwater plants or debris (Waite 1928; Martin *et al.* 1966; Tyler and Davies 1978; Bell 1982a,b; Martin and Littlejohn 1982; Cree 1984; Hero *et al.* 1991). Egg capsules are relatively small (2-2.5

mm across), with their enclosed eggs about 1.3–1.5 mm in diameter and having a black upper pole (Martin and Littlejohn 1966; Tyler and Davies 1978; Bell 1982a,b; Hero *et al.* 1991).

Tadpoles are quite variable in appearance. Newly hatched tadpoles may appear greyish-black (Bell 1982a) or dark brown with well developed external gills (Martin and Littlejohn 1982). Older tadpoles have been variously described as being dark velvety black-brown (Bell 1982a), green (Waite 1928), light yellowish grey with a darker intestinal mass (Bell 1982a; Martin and Littlejohn 1982), pinkish with yellowish fins (Hero *et al.* 1991) and pinkish-grey with a yellowish tail (Martin 1965). They develop a yellowish-pink sheen (Bell 1982a) or golden-coloured markings (Waite 1928) on the abdomen before leaving the water. Tadpoles have two upper and three lower rows of labial teeth, the

inner row in each labium being divided, with a narrow band of papillae bordering the sides and back of the mouth disc (Martin 1965; Martin and Littlejohn 1982). Martin (1965) has provided illustrations of both a lateral view and the mouth disc of these tadpoles.

Adults of both *L. raniformis* and *L. aurea* secrete copious quantities of mucus that is, at least to humans who are handling these frogs, unpleasant smelling and tasting, and severely irritating if it contacts the lips or eyes (Pyke and White 2001; Pyke pers. obs.). It is also toxic to other frogs enclosed in the same container (Martin and Littlejohn 1982).

Distribution

The original distribution of *L. raniformis* included parts of mainland Australia, Tasmania, King Island and Flinders Island (Fig. 1; Copland 1957; Littlejohn and Martin 1965; Littlejohn

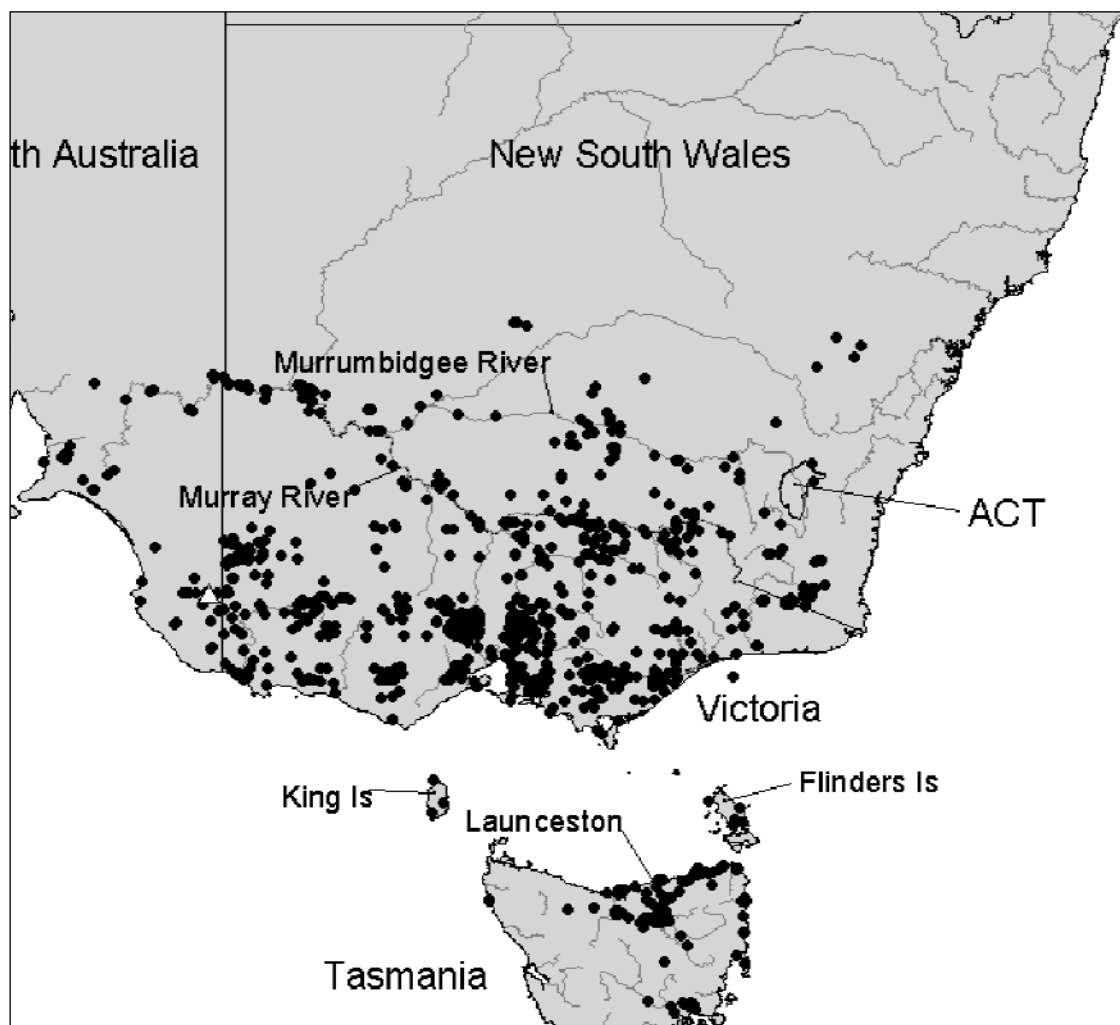


Figure 1. All recorded locations of *Litoria raniformis*. These were obtained by combining location records from databases held by Australian Museum, NSW National Parks & Wildlife Service, Tasmanian Parks and Wildlife, Atlas of Victorian Wildlife, Museum of Victoria, and South Australian Museum, along with information presented in Ashworth (1998). Location of fossil record reported in Tyler and Barrie (1996) is shown by open triangle.

1966; Courtice 1972; Brook 1975; Courtice and Grigg 1975; Barker and Grigg 1977; Tyler 1978; Tyler and Davies 1978; Martin and Littlejohn 1982; Cogger *et al.* 1983; Hoser 1989; Osborne 1990, 1992; Bennett *et al.* 1991; Ayers 1995; Ehmann and White 1997; Sadlier *et al.* 1996; Cogger 2000). Prior to European settlement of Australia, the mainland distribution extended from about the Bathurst region of the western slopes of the Great Dividing Range in New South Wales southward through the southern tablelands of New South Wales and the Australian Capital Territory, through central Victoria (excluding mallee) to the Victorian coast west of about Orbost, through western Victoria to about the Murray River, and into south-eastern South Australia near the mouth of the Murray River (Fig. 1). This species also occurred in Tasmania, especially near the east and north coasts, but also in a few more central

sites and in one apparently isolated area on the west coast (Fig. 1; Ashworth 1998). The original elevation range of the species extended from about sea level to about 1,000 m (Ehmann and White 1997).

The natural distribution of *L. raniformis* has declined, most noticeably since about 1990. Since then it has apparently disappeared from the western slopes and southern tablelands of New South Wales and the Australian Capital Territory, from much of central Victoria and from parts of Tasmania and South Australia (Osborne 1990, 1992; Rounsevel and Swain 1993; Bennett 1997; Mahony 1997; Tyler 1997; Ehmann and White 1997; Ashworth 1998; White and Pyke 1999), and has declined in other regions (Osborne 1992; Tyler 1997). During this period the species has been recorded in New South Wales from about 20 sites, mostly along the Murrumbidgee and Murray Rivers, but also within irrigated areas

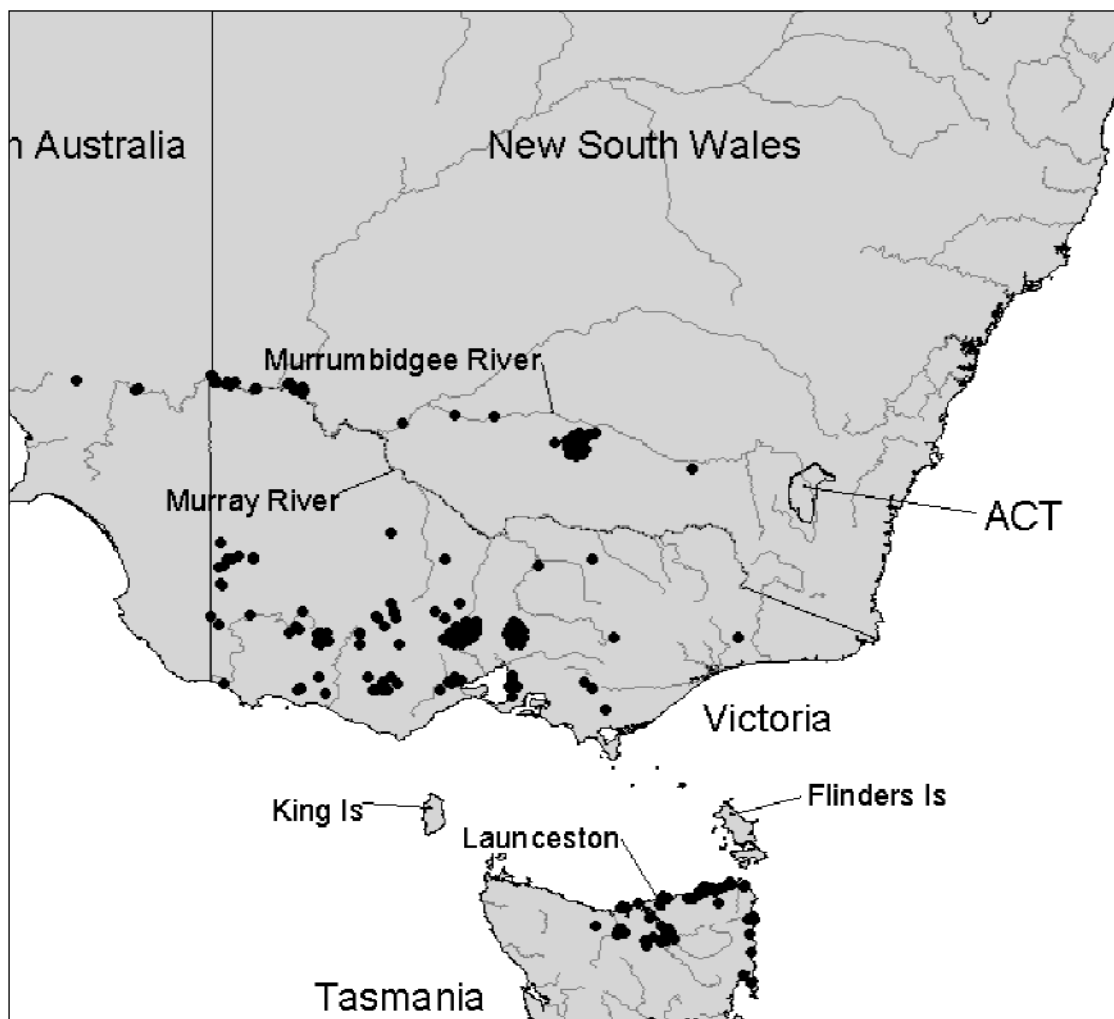


Figure 2. Locations for *Litoria raniformis* recorded after 1989. These were obtained by combining databases used for Figure 1 with locations recorded in AMBS Consulting (2000) and Ashworth (1998), and with unpublished location information provided by Arthur White in relation to locations listed in Ehmann and White (1997).

near these rivers (Fig. 2; Ayers 1995; Ayers *et al.* 1995; Ehmann and White 1997; Sadler *et al.* 1996; Mahony 1997; AMBS Consulting 2000). During the same period, it has been recorded from about 190 sites in Victoria, distributed mostly through the central and southwest parts of the state (Fig. 2), and has disappeared from King and Flinders Islands, and from the north-west and central midlands of Tasmania (Ashworth 1998). During this period it has been recorded at about 100 sites in Tasmania, mostly along the eastern coast and around Launceston in the north (Fig. 2) and Ashworth (1998) found breeding populations at just 17 of these sites. The species has not been recorded since 1990 in the Australian Capital Territory, King Island or Phillip Island and is presumably extinct in these areas (Osborne 1990; Ashworth 1998). In New South Wales and Tasmania the species has not recently been found at elevations higher than about 200 m (Ehmann and White 1997; Ashworth 1998; AMBS Consulting 2000).

These apparent declines are unlikely to be the result of inadequate recent frog surveys in places where *L. raniformis* might occur. Since 1990 frog surveys have been carried out in areas of suitable habitat for this species throughout much of New South Wales, South Australia and Tasmania and many former locations for the species in these areas have been revisited during this period without finding it (e.g., Ehmann and White 1997; Tyler 1997; Ashworth 1998; White pers. comm.). Similar disappearances have been recorded in Victoria (G. Gillespie pers. comm.; A.A. Martin pers. comm.). On the other hand, since there were relatively few frog surveys in these areas prior to 1990, it is possible that the original distribution was more extensive than indicated by available location records.

With human assistance, there have been some expansions of the distribution of *L. raniformis* within and near its natural range. The species was, for example, translocated into the grounds of the Defence Research Establishment at Salisbury in South Australia from a nearby site (Tyler 1979). It has also spread into artificially created wetlands and moats at Victoria's Open-Range Zoo near Werribee, Victoria (A.A. Martin pers. comm.) and into artificially irrigated areas such as the Coleambally Irrigation Area near Griffith, New South Wales (Ehmann and White 1997; AMBS Consulting 2000).

The distribution of *L. raniformis* has further expanded through its successful introduction to

New Zealand. Individuals of this species were translocated from Hobart in Tasmania to Canterbury on the south island of New Zealand in about 1867 (Marriner 1907; Thomson 1922; McCann 1961; Tyler 1979; Bell 1982a; Gill 1986). Since then the species has become, with human assistance, widely distributed through both the North and South Island (Thomson 1922; McCann 1961; Bell 1982a,b; Cree 1984; Ford 1986; Gill 1986; Pickard and Towns 1988) and on the offshore island of Great Barrier (Bell 1982a).

It is not clear how the distribution of *L. raniformis* has varied over geological time. It is possible that *L. raniformis* and *L. aurea* separated evolutionarily from one another during a time when Tasmania and mainland Australia were separated by water, with *L. raniformis* initially restricted to Tasmania, but spreading into the mainland when sea level was lower and there was no such water barrier (Watson and Littlejohn 1985). It is also possible that these two species initially separated on either side of the Eastern Highlands with *L. raniformis* to the west and *L. aurea* to the east (Littlejohn 1967). Remains of *L. raniformis* have been found at Henschke's Cave in South Australia in fossil deposits with an estimated age of between 35 and 100 thousand years (Tyler and Barrie 1996). This site is within the range of locations that have been recorded over about the last 100 years (Fig. 1).

Taxonomy and phylogeny

Litoria raniformis was originally described by Keferstein (1867). However, in 1957 what we now recognise as the species *L. raniformis* was considered to be two subspecies of the species *L. aurea*. The subspecies *L. a. raniformis* corresponded to the mainland portion of the current species *L. raniformis*, while the subspecies *L. a. major* was the Tasmanian portion (Copland 1957; Martin and Littlejohn 1982). These two sub-species are, however, no longer recognised (Moore 1961; Courtice 1872; Courtice and Grigg 1975; Martin and Littlejohn 1982). In 1957 two additional subspecies of *L. aurea* were recognised, namely *L. a. aurea* and *L. a. ulongae*, but these were subsequently combined into a single subspecies *L. a. aurea* (Copland 1957; Courtice 1972). In 1972 the two recognised subspecies of *L. aurea* were elevated to become the two species *L. aurea* and *L. raniformis* (Moore 1961; Littlejohn 1963; Courtice 1972; Courtice and Grigg 1975; Bell 1982a; Martin and Littlejohn 1982). These two species are recognisably different on the basis of morphology, dorsal appearance and call (Bell 1982a; Thomson *et al.*

1996). That these are two distinct species has now also been demonstrated by in-vitro-fertilisation experiments, electrophoretic studies, serum albumin and protein variation (Courtice 1972; Courtice and Grigg 1975; Maxson *et al.* 1982; Sherwin 1995). Wells and Wellington (1985) proposed that populations in Tasmania be considered a separate species under the name *Ranoidea major*, but their recommendations have not been adopted.

Interpretation of information about *L. raniformis* is complicated by the confusion of identification between this species, *L. aurea* and *L. castanea* (Tyler 1997; White and Pyke 1999). Because of the changing taxonomy some studies involving *L. raniformis* have, for example, adopted the species name *L. aurea* (Bell 1982a). For example, some of the early studies must have included *L. raniformis*, by virtue of where frogs were found or their appearance, but used only the species name *L. aurea* (Krefft 1866; Spencer 1888; Sweet 1896, 1907; Fletcher 1892, 1897; Marriner 1907; Horning 1927; Waite 1928; Fleay 1935; Parker 1938; Richardson 1943, 1947, 1952; Copland 1957; Richardson and Barwick 1957; McCann 1961; Moore 1961). Some observations that were believed to be of *L. raniformis* were probably *L. castanea* (see White and Pyke 1999).

Litoria raniformis is presently considered to be a member of the *Litoria aurea* group of six or seven closely related species within the relatively large genus *Litoria*. This group is usually considered to include *L. albogutta*, *L. aurea*, *L. castanea* (= *L. flavipunctata*), *L. cyclorhynchus*, *L. dahli*, and *L. moorei*, although *L. alboguttata* is not always included (Tyler and Davies 1978; King 1980; Maxson *et al.* 1982; Tyler 1982; Thomson *et al.* 1996; White and Pyke 1999). The *L. aurea* species group is considered monophyletic (King 1980), while the genus as a whole is believed to be polyphyletic (King 1980; 1993). Within the genus *Litoria* there are presently about 88 recognised Australopapuan species in 36 species groups (Tyler 1978).

Within the *L. aurea* species group, *L. raniformis* is apparently more closely related to *L. castanea* than to *L. aurea*, and more closely related to *L. aurea* than to other frog species besides *L. castanea*. Albumin immunological distance data indicate that *L. raniformis* shows no differentiation from *L. castanea* and therefore that these two species separated relatively recently, but that *L. raniformis* separated from *L. aurea* about 1.1 million years ago (Roberts and Maxson 1988). A quantitative micro-

complement fixation technique using serum albumins has suggested that *L. raniformis* is more closely related to *L. aurea* than to other frog species, but this study did not consider *L. castanea* (Maxson *et al.* 1982). A satisfactory speciation model for the species group has not been developed (Roberts and Maxson 1988).

Dichotomous keys have been developed for the separation of *L. raniformis* from other frog species (Copland 1957; Tyler 1978; Martin and Littlejohn 1982), other congeneric frog species (Waite 1928), and other members of the same species complex (Thomson *et al.* 1996).

Hybridisation and sub-specific variation

L. raniformis has been reported to co-occur with the closely-related *L. aurea* at many sites with little or no signs of hybridisation between the two species. They are presently found together at sites in East Gippsland in Victoria (Littlejohn *et al.* 1963; Courtice 1972; Courtice and Grigg 1975; Brook 1975; Littlejohn and Watson 1993; Tyler 1997) and in the north island of New Zealand (Bell 1982a,b; Pickard and Towns 1988). In the past they occurred together at sites around Canberra on the southern tablelands (Courtice 1972; Osborne 1990) and may also have co-occurred around Bathurst and other parts of the western slopes of the Great Dividing Range in New South Wales (White and Pyke 1999). Yet, in the wild, few possible hybrids have been observed (Sherwin 1978; Littlejohn and Watson 1993; Gillespie 1996; Tyler 1997) and it is generally not difficult to separate the species (Littlejohn *et al.* 1963; Courtice 1972; Courtice and Grigg 1975; Bell 1982a). The only indication of possible hybridisation has been the production of viable offspring from a laboratory mating between a *L. raniformis* female and a *L. aurea* male (Bell 1982a).

It is not known what mechanisms limit or prevent such hybridisation, but their distinctively different calls may be involved (Courtice 1972). Consistent with this is the report that the calls of the two species seemed more different when they were sympatric than when they were allopatric (Ford 1983).

No geographic variation amongst populations of *L. raniformis* has been reported and no subspecies are currently recognised (Tyler 1997). Populations on King and Flinders Islands show no apparent divergence in morphology from populations on the Tasmanian mainland, though these populations must have been isolated from one another for about 10,000-11,000 years (Littlejohn and Martin 1965).

Sex/age categories

Sex/age categories have not been precisely defined. Males probably develop their 'nuptial pads' upon reaching adulthood, as do males of *L. aurea* (Pyke and White 2001). Hence males with these pads can presumably be classified as adult (e.g., Ashworth 1998). As males apparently develop these pads at about 55 mm, frogs that are this large or larger and lack such pads can be identified as females. The snout-vent length (SVL) at which females attain maturity is unknown but it is likely to be greater than 55 mm (see below). Hence it is only possible to recognise three sex/age categories, namely immatures, adult males and large females, with the last category including both immature and adult females.

Habitat

The patterns of habitat use are poorly understood. This species has generally been reported to occur in or around water that is shallow and still or slowly moving, often with emergent aquatic vegetation, but the array of reported breeding habitats is so broad that it provides little further information concerning habitat use. These include lakes or reservoirs; lagoons; marshes, swamps or wetlands; ponds, ditches and other artificial depressions; farm dams; areas which receive artificial flood-irrigation; as well as still backwaters and other sluggish areas of rivers and streams (Littlejohn 1963; Martin 1965; Courtice and Grigg 1975; Tyler 1978, 1997; Hobbs 1980; Bell 1982a,b; Martin and Littlejohn 1982; Cogger *et al.* 1983; Cree 1984; Gill 1986; Hoser 1989; Osborne 1990, 1992; Bennett *et al.* 1991; Hero *et al.* 1991; Tyler 1992, 1997; Rounsevel and Swain 1993; Ayers 1995; Sadlier *et al.* 1996; Ehmann and White 1997; Ashworth 1998; AMBS Consulting 2000).

In most cases emergent aquatic vegetation has been present (e.g., Martin 1965; Courtice and Grigg 1975; Tyler 1978; Hobbs 1980; Martin and Littlejohn 1982; Hoser 1989; Osborne 1990; Ayers 1995; Ehmann and White 1997; Ashworth 1998) but in a few cases there has been no such vegetation (e.g., Ashworth 1998). Nearby terrestrial vegetation has been reported to include grassland, shrubland, woodland or forest (Hobbs 1980; Cogger *et al.* 1983; Hero *et al.* 1991; Tyler 1992; Ayers 1995; Ehmann and White 1997). Water bodies with *L. raniformis* present have had pH ranging from 5.6 to 8.4 and electrical conductivity from 101 to 4800 μS (Ashworth 1998). Tadpoles have been found in water ranging in temperature from about 16 to

20° C. (Cree 1984). This information provides little basis on which to predict presence/absence of the species.

It is also unclear to what extent *L. raniformis* breeds in water bodies that may be viewed as 'permanent' as contrasted with 'semi-permanent' or 'ephemeral'. A number of authors have reported that the species occupies permanent water bodies (Littlejohn 1963; Martin 1965; Courtice and Grigg 1975; Tyler 1978, 1992; Martin and Littlejohn 1982; Cree 1984; Hero *et al.* 1991; Osborne 1992; Tanton 1994; Sadlier *et al.* 1996; Ashworth 1998), but none of these has defined what they mean by 'permanent' and none has presented information in relation to the degree of water permanence at any site. In addition many sites where this species breeds clearly experience a high level of variability in water level (e.g., Hobbs 1980; Ehmann and White 1997; Pyke pers. obs.) and the timing of breeding appears to be strongly related to the timing of the flooding cycle (Ehmann and White 1997). It is therefore possible that, like *L. aurea*, this species does best in water bodies that are either ephemeral or fluctuate significantly in water level (cf. Pyke and White 1996).

Like the closely-related *L. aurea*, *L. raniformis* sometimes occurs and successfully breeds within sites that are largely or completely human-made. For both species such sites include farm dams, garden ponds and quarries (Littlejohn 1963; Martin 1965; Courtice and Grigg 1975; Bell 1982a,b; Martin and Littlejohn 1982; Cree 1984; Gill 1986; Hoser 1989; Osborne 1990, 1992; Bennett *et al.* 1991; Hero *et al.* 1991; Tyler 1992, 1997; Ayers 1995; Sadlier *et al.* 1996; Ehmann and White 1997; Ashworth 1998). *Litoria raniformis* also breeds in areas that are artificially flooded through irrigation (Tyler 1997; Ehmann and White 1997; AMBS Consulting 2000). This extensive use of human-made sites has important potential consequences in terms of conservation and management of the species (see below).

B. Individual

Physiology

Individuals of *L. raniformis* are exposed to a wide range of environmental conditions. They may be found in water, on the nearby ground or on low vegetation (e.g., Courtice 1972; Courtice and Grigg 1975), they may be active either during the night or in the daytime (e.g., Barker and Grigg 1977; Hoser 1989; Ashworth 1998), they are often observed 'basking' in the sun during

the day (e.g., Courtice 1972; Courtice and Grigg 1975; Barker and Grigg 1977; Bell 1982a,b; Martin and Littlejohn 1982; Hoser 1989; Bennett *et al.* 1991; Ayers 1995; Ashworth 1998), ambient temperatures at which they are encountered may range from about 0 to 40°C (Cree 1984; AMBS Consulting 2000), and both flood and drought conditions sometimes prevail in areas where they occur.

Litoria raniformis has physiological characteristics that reflect both its aquatic tadpole phase and its more terrestrial adult phase. Its tadpoles, for example, show ammonotelic nitrogen excretion, reflecting their aquatic lives at this stage, whereas metamorphosed frogs are strongly ureotelic which is characteristic of a more terrestrial existence (Cree 1985). In this regard it is similar to most other frog species (A.A. Martin pers. comm.). In addition, adults are able to relatively quickly absorb water through their ventral surface and hence able to rapidly re-hydrate after periods 'basking' in the sun or otherwise out of the water (Cree 1985, 1988).

The species is physiologically affected by ambient temperature. Metabolic rate has been found to decrease as temperature decreased from 23 to 7°C, and individuals were found to be physically active at both 23 and 15°C but not at 7°C (Cree 1984). It has also been suggested that this species 'hibernates' during the winter at some sites (e.g., Cree 1984; Ayers 1995; Ashworth 1998), but no study has yet demonstrated that this occurs.

The species may also be adapted behaviourally and physiologically to deal with very dry conditions. Sometimes when their habitat has dried out they have been found sheltering within clumps of dried mud (e.g., Thomson 1922) that have presumably retained more moisture than other nearby situations. It has also been suggested that the species will 'aestivate' during dry conditions (Ashworth 1998), but so far there is no supporting physiological evidence.

One study has considered the physiology of food intake. Cree (1985) found that recently metamorphosed *L. raniformis* frogs excreted nitrogen in both ammonia and urea and that, while diet had no effect on the relative amounts of ammonia and urea excretion, it did affect the absolute levels of nitrogen excreted. Frogs that were fed on both flies and mealworms excreted more nitrogen than frogs that were fed just flies (Cree 1985).

Growth, development and morphology

During the egg/tadpole phase, growth and development are variable and tadpoles may reach large total length before metamorphosis. Eggs hatch within 2-4 days of laying (Ehmann and White 1997). Metamorphosis generally occurs within about 3 months of hatching, by which time tadpoles have attained a total length of about 80-100 mm (Martin 1965; Barker and Grigg 1977; Tyler 1978; Bell 1982a,b; Martin and Littlejohn 1982; Cree 1984; Gill 1986; Hero *et al.* 1991), sometimes having reached 130-150 mm (Bell 1982b; Gill 1986). SVL at metamorphosis is probably about 25-35 mm in general as this is the range exhibited by recently metamorphosed frogs (Martin 1965; Tyler 1978; Bell 1982a; Martin and Littlejohn 1982) and Cree (1984) recorded SVLs for four metamorphosing frogs that ranged from 29 to 33 mm. Strangely, however, Copland (1963) reported SVLs for several metamorphosing frogs captured on land that were between 14 and 16 mm, stated that he had recorded even smaller metamorphosing individuals, and did not observe any such individuals with SVL greater than about 26 mm. Although tadpoles generally complete development during the summer or autumn of the breeding season in which they hatch (Cree 1984), they may overwinter as tadpoles under some circumstances and hence take about a year from hatching to metamorphosis (Martin 1965; Tyler 1978, 1992; Martin and Littlejohn 1982).

Little or no increase in SVL apparently occurs during the relatively brief metamorphosing component of the metamorphosing/frog phase. Cree (1984) reported that, for a group of four individuals that were kept outdoors, SVL remained nearly constant for the period of 3-4 days whilst the tail was resorbed.

The pattern of growth of frogs is unclear. Ashworth (1998) found that, after metamorphosis, frogs continue to grow for about the next 12 months, but may grow relatively little after that. He observed ultimate SVLs of only about 70 mm for wild-caught frogs that were estimated to be six years old (Ashworth 1998). Similarly Bell (1982a) reported that one captive individual took 4 years to attain a size of 68 mm. However, observed SVLs are commonly larger than those observed by Ashworth (1998), suggesting either that growth may occur over periods of more than 12 months or that there are geographic differences in maximum SVL. SVL for this species generally ranges up to about

80-90 mm (Littlejohn 1963; Courtice 1972; Hobbs 1980; Bell 1982b; Gill 1986; Ashworth 1998) and may occasionally reach 100 mm or more (Tyler 1978; Hoser 1989).

On average females apparently grow to larger sizes than males, and this is also the case for the closely related *L. aurea*. Reported maximum SVLs have been 65-75mm for males and 82-104mm for females (female max. 82 mm, male max. 65 mm, Littlejohn 1963; female 92 mm, male 65 mm, Gill 1986; female 104mm, male 65 mm, Tyler 1978; female 85 mm, male 75 mm, Ashworth 1998).

Litoria raniformis and *L. aurea* are similar in size at all stages of growth and development (see above and Pyke and White 2001), although it has been suggested that *L. raniformis* might be a little larger than *L. aurea* (Bell 1982a). Tadpoles of both species may reach often 100 mm in total length and occasionally attain even greater lengths. The average SVL at metamorphosis may be greater for *L. raniformis* than for *L. aurea*, as the generally observed range for *L. raniformis* encompasses higher values than that for *L. aurea* (i.e., 25-35 mm vs. 20-30 mm), but there is much overlap between the two species in size at metamorphosis and no quantitative comparison has been made. The maximum observed SVL for adults is about 100 mm for both species.

The sizes and/or ages at which males and females become reproductively mature are unknown. The SVL at which the males develop 'nuptial pads' and presumably reach adulthood must be about 55 mm as individuals this large and larger have been sexed (Courtice 1972; Tyler 1978; Barker *et al.* 1995; Ashworth 1998). Cree (1984) considered that individuals less than 40 mm in SVL were immature, but did not present any evidence in support of the particular threshold. The body size at which females attain maturity is unknown, although it is likely to be as large as or larger than this male threshold as females are generally observed to be as large as or larger than males (e.g., Ashworth 1998). Female *L. aurea* mature at a larger size than do males (Pyke and White 2001).

Low frequencies of developmental abnormalities in *L. raniformis* have been detected. Of the large numbers dissected in teaching laboratories in New Zealand, about 0.3% have been found to have an external hernia (Richardson 1943, 1947) and another 0.06% had a different kind of hernia in which the ovarian fat-body extends across the abdominal cavity, without adhesion to or involvement of other viscera, to perforate the linea alba and expand into the ventral lymph-

space (Richardson 1952). In addition, in over 6,000 specimens, one individual was found in which faulty eruption of the right fore-limb had resulted in the limb being located in subcutaneous lymph-spaces and enclosed in a non-adherent fold of skin (Richardson 1947; Richardson and Barwick 1957).

Despite the large numbers of *L. raniformis* that have been dissected, the internal anatomy and morphology have been little reported. Sweet (1896) described the spinal nervous system, with comments on variation amongst individuals.

Reproduction

Most breeding activity occurs from about August or September to about January or February (Ashworth 1998). Calling by males and mating have generally been recorded during this period (Littlejohn and Martin 1965; Littlejohn 1966; Brook 1980; Bell 1982b), although they have also occasionally been recorded during March or April (Brook 1980; Cree 1984; G. Muir and E. Magarey, Australian Museum Business Services, pers. comm. 2001). Tadpoles have generally been observed from September to April (Brook 1980; Bell 1982b; Cree 1984) and immature frogs have generally been observed during January to April (Cree 1984).

Males may call by day or by night (Bell 1982a; Ashworth 1998), while either floating in areas of open water or sitting on the ground adjacent to the water (Littlejohn 1963, 1966; Littlejohn and Martin 1965; Bell 1982a; Martin and Littlejohn 1982; Cree 1984; Gill 1986; Hero *et al.* 1991). Calling intensity is variable but is generally restricted to warm and calm conditions (Ashworth 1998). Water temperatures at times of calling have been found to range between about 11 and 16°C (Littlejohn and Martin 1965; Martin and Littlejohn 1982; Cree 1984). Males sometimes call independently of one another but often call as part of a group chorus (Littlejohn and Martin 1965; Brook 1980; Bell 1982a; Ehmann and White 1997). Mating and spawning have also been observed both during the day and at night (Bell 1982a).

Amplexus in *L. raniformis* is in the pectoral position with the males hugging the females from behind, just below the females' arms (Bell 1982a).

There is currently no documented information concerning clutch size, but judging from the number of ovarian eggs in dissected mature females it is likely to be at least several hundred (A.A. Martin pers. comm.). If similar to that for *L. aurea*, average clutch size for *L. raniformis* could number in the thousands (Pyke and White 2001).

General behaviour and activity patterns

Frogs of this species are generally more active and more often observed at night during the period from spring to autumn, than either during the day or during the winter months (Barker and Grigg 1977; Bell 1982a,b; Cree 1984; Gill 1986; Hoser 1989; Hero *et al.* 1991; Ayers 1995; Ashworth 1998). Reported night-time observations have been of frogs floating in the water or sitting on the ground (Littlejohn 1963; Barker and Grigg 1977; Bell 1982b; Cree 1985, 1988; Hero *et al.* 1991). During the day they are, however, often observed 'basking' in the sun while either sitting on emergent vegetation or on the ground, and they are sometimes heard calling (Barker and Grigg 1977; Martin and Littlejohn 1982; Ayers 1995; Ashworth 1998). When approached these frogs typically dive into adjacent water (Waite 1928; Hobbs 1980; G. Pyke pers. obs.). They are also sometimes observed during the winter, especially during relatively warm conditions (Cree 1984). Cree (1984) found that they became inactive as temperature dropped from 23 to 7°C. Shelter sites used by individuals when they are inactive and out of sight include cracks in the soil, rocks, fallen timber, thick vegetation or other debris (Bell 1982b; Tyler 1992; Ehmann and White 1997).

Litoria raniformis is not a frequent climber and frogs of this species are usually found in water or on nearby ground level (Waite 1928; Martin and Littlejohn 1982; Gill 1986; Ayers 1995; Pyke pers. obs.). Occasionally, however, it will climb a relatively short distance up reeds or other emergent aquatic vegetation (Hobbs 1980; Ayers 1995; Pyke pers. obs.). It is reportedly less agile at climbing amongst emergent vegetation than the closely-related *L. aurea* (Barker and Grigg 1977).

Tadpoles of this species can be observed both night and day, as they generally swim near the water surface (Martin 1965). They have been described as very fast moving (Hoser 1989).

Movements

Little is known about the movements of *L. raniformis*. They must move between shelter sites, where they are inactive and out of sight, to sites where they are either 'basking' or active. They have been observed on roads or in other locations away from water bodies, especially during rainy weather (Barker and Grigg 1977; Bell 1982b; Martin and Littlejohn 1982; Ayers 1995; Ehmann and White 1997; Pyke pers. obs.), and were sometimes the most common frog seen on roads on warm, wet nights (A.A. Martin pers.

comm.). These observations are generally interpreted as being a consequence of 'overland movement' or 'dispersal' (Barker and Grigg 1977; Bell 1982b; Ayers 1995). According to Hoser (1989), however, such observations are rare, even where the species is common.

Foraging and diet

Very little is known about the foraging and diet of *L. raniformis*. Frogs of this species are reported to forage in the wild both during the day and at night (Cogger *et al.* 1983), to feed on tadpoles and other frogs, including members of the same and other species (Thomson 1922; Barker and Grigg 1977; Martin and Littlejohn 1982; Hero *et al.* 1991; E. Magarey, pers. comm. 2001), to feed on other vertebrates such as lizards, snakes and small fish (Martin and Littlejohn 1982), and to feed on invertebrates (Ayers 1995). It has been labelled an opportunistic forager (Ayers 1995). In captivity individuals have mostly been recorded eating various insects, including flies (Thomson 1922; Cree 1985), beetles (Robinson 1993), beetle larvae (Cree 1985), and grasshoppers (Robinson 1993), but have also been recorded feeding on small snakes (Fleay 1935; Copland 1957) and possibly water snails (Robinson 1993). Cogger *et al.* (1983) considered this species to be a generalist carnivore. Tadpoles of this species have been maintained in captivity on a diet of *Elodea* sp. and boiled lettuce leaves (Cree 1984).

Other behaviour

In addition to mating calls, males have been reported to emit a cat-like yowl or scream, with their mouths wide open, when picked up or roughly handled (Martin and Littlejohn 1982; A.A. Martin pers. comm.). Females may give similar calls, as in *L. aurea* (Pyke and White 2001).

Individual frogs may remain in specific locations that they use for one activity or another. Bell (1982a) observed that individual males generally called from the same area of pond surface, and that adults of both sexes tended to utilise the same marginal sites for basking.

Population biology

Abundance and population genetics

There have been no published quantitative assessments of population size for *L. raniformis*. There is, however, general agreement that this species has been relatively abundant in some locations. According to Krefft (1866) it was, along with other members of the *Litoria aurea*

species group, the most 'commonly' encountered of Australia's frogs and was readily collected as food by aboriginal people. It is considered to have formerly been 'common' in lowland areas and on offshore islands of Tasmania (Martin and Littlejohn 1982; Ashworth 1998), in the Southern Tablelands of New South Wales and the Australian Capital Territory (Osborne 1990, 1992), and in New Zealand (Thomson 1922), and 'abundant' along the Murray River in southwest New South Wales (Ayers 1995). In New Zealand in about 1980 it could be seen in 'large numbers' at breeding ponds or on roads at night (Bell 1982b) and, at least until the 1950s, it could be caught in sufficient numbers to be used for dissection in laboratory teaching classes (Richardson 1943, 1947, 1952; Brace *et al.* 1953). During the 1940s, for example, about 100 were dissected each year in zoology laboratories in Victoria University College in Wellington (Richardson 1952). More recently it was described as being 'common' and 'easy to catch' at some sites in Victoria (Osborne 1990; Bennett *et al.* 1991; Hero *et al.* 1991) and as having 'robust' populations in the Murray River valley (Mahony 1997). In 1992 Tyler considered this species to be generally 'abundant' (Tyler 1992).

There has been no suggestion that the abundance of *L. raniformis* at any site has decreased to some new lower level than in the past. Instead the species has reportedly either remained 'abundant' or disappeared completely from some sites. This could, however, reflect a bias in reporting abundance as complete disappearance is probably considerably more conspicuous than population declines.

There is no available information concerning many aspects of the population biology of the species, including the sex/age structure, temporal (seasonal, yearly, long-term) patterns and genetic structure of populations.

Regulating factors

Population size in *L. raniformis* could be influenced by a variety of factors, including nature and extent of suitable habitat, predation, parasites, pathogens, UVB radiation levels, temperature, cattle grazing, pollution, salination and rainfall (Ayers 1995; Tyler 1997; Ehmann and White 1997; Ashworth 1998). Many wetlands have been replaced or modified by other land uses such as agriculture and urban development, thus decreasing the quality and extent of suitable habitat (Rounsevel and Swain 1993; Ayers 1995;

Ehmann and White 1997; Ashworth 1998; White and Pyke 1999). Frogs may fall prey to a number of different kinds of animal especially the introduced European Fox (*Vulpes vulpes*) (Tyler 1997; Bell 1982a). The introduced Plague Minnow has been implicated in the decline of *L. raniformis* (Mahony 1997; Tyler 1997; Ehmann and White 1997; White and Pyke 1999) and eggs and tadpoles of this species are likely to be eaten by this and other fish species, as well as by various kinds of birds and invertebrates. A number of different parasites are known to infect *L. raniformis* (Raff 1911, 1912; Horning 1927; Brace *et al.* 1953; Delvinquier 1988). Chytrid fungus and other pathogens have been implicated in the declines of frog species worldwide (e.g., Blaustein *et al.* 1994; Anderson 1998; Berger and Speare 1998) and chytrid fungus has recently been found to be present and associated with sick frogs in populations of both *L. raniformis* and *L. aurea* (Porter 1999; Bishop 2000). The level of UVB radiation, which is being influenced by various human-enhanced emissions into the atmosphere, has been shown to influence survivorship, growth and development in tadpoles of some frog species (van de Mortel 1988; Broomhall *et al.* 2000) and frog species such as *L. raniformis* that 'bask' in the sun may be especially susceptible to any effects of UVB radiation on adults (Tyler 1997). Human-induced 'global warming' may also affect tadpoles through increases in average water temperature (e.g., Cree 1984), and bioclimatic analysis has suggested that further global warming is likely to reduce the overall distribution of *L. raniformis* (Ashworth 1998; Bennett *et al.* 1991). Cattle and other livestock, through their trampling of vegetation, may reduce the areas available for foraging or shelter (Ayers 1995; Ehmann and White 1997; Ashworth 1998). It has been suggested that a herbicide containing a dispersant is directly responsible for some declines of *L. raniformis* where it has been used around dams (Tyler 1997). Salination of some billabongs in Murray Valley has been considered a severe threat to the species (Ehmann and White 1997). Lack of standing water may reduce reproduction, lack of moisture may reduce adult survivorship, and drought conditions may have played a role in declines of *L. raniformis* in the southern tablelands and in Tasmania (Osborne 1986, 1990, 1992; Tyler 1997; Ashworth 1998). However none of these factors has been investigated in detail and it is not clear whether any of them may have a density-dependent or regulating effect on populations of *L. raniformis*.

Community biology

Little is known about the extent to which other frog species co-occur with *L. raniformis*. It is the only frog species present at many sites in New Zealand and in the other Pacific islands where it has been introduced (Bauer and Sadlier 2000). However, at most sites where it occurs, it co-occurs with other frog species (e.g., Thomson 1922; AMBS Consulting 2000; Pyke pers. obs.). At some sites in New Zealand and Victoria it co-exists with its sister species *L. aurea* (Courtice 1972) and, at some sites on the southern tablelands and western slopes of the Great Dividing range, it may have co-existed with up to two other species from the *Litoria aurea* species group (Courtice 1972; Thomson *et al.* 1996).

Similarly little is known about interactions between *L. raniformis* and other animal species. It could influence other frog species either as a predator (e.g., Thomson 1922) or a competitor, and it may have displaced *L. ewingii* from some sites in New Zealand (Thomson 1922). It has had a deleterious effect on hatching success and nestling survival in Clamorous Reedwarblers (*Acrocephalus stentoreus*) and Little Grassbirds (*Megalurus grammineus*) through congregating in nests of these two bird species (Hobbs 1980). In the latter case, an area of *Typha* sp., in which these birds were nesting, became a refuge site for large numbers of frogs that were dispersing from the nearby bed of a lake in which very successful breeding by the frogs had just occurred, but which was now drying up (Hobbs 1980).

Research techniques and captive husbandry

Compared with many other frog species, *L. raniformis* are conspicuous and relatively easy to catch (Martin and Littlejohn 1982). Like the closely-related *L. aurea*, frogs of this species are often found in the open, either floating in water, sitting on reeds or sitting on the ground. Under these circumstances individuals can be captured using the "stalk and lunge" method employed with *L. aurea* (Pyke & White 2001). Considerable stealth may, however, be necessary as they will often jump into water when approached (Hobbs 1980; Pyke pers. obs.).

Frogs of this species may also be captured by searching under potential shelter material (and lunging at any observed frogs) and in pit-traps. This species shelters under a variety of materials and has been found by lifting up such cover (Bell 1982b; Cree 1984; Ayers 1995; Ashworth 1998). Humphries (1979) captured the closely-related *L.*

aurea and *L. castanea* (called *L. raniformis* in his thesis but later identified as *L. castanea/flavipunctata* by Thomson *et al.* 1996) using a drift-fence and pit-traps. Each pit-trap consisted of a 25-litre polyethylene container, buried in the ground with the opening at ground level and with a funnel inserted in the opening and projecting down into the container. The resulting arrangement resembled the 'one-way' entrance employed in some fish traps. However, using pit-traps that were simple cylinders, 11 cm deep and 10.5 cm in diameter, at a site where *L. aurea* was abundant, Miehs (2000) did not capture any frogs. Once captured, frogs of *L. raniformis* may, in identical fashion to *L. aurea*, be kept in moist plastic bags while waiting to be examined and held by hand during examination (Pyke pers. obs.).

Body length for frogs of *L. raniformis* has been measured in two slightly different ways: tip of the snout to the end of the free portion of the urostyle (e.g., Richardson 1947, 1952; Richardson and Barwick 1957); tip of the snout to the vent (e.g., Littlejohn 1963; Courtice 1972; Hobbs 1980; Bell 1982a, b; Cree 1984; Gill 1986; Ashworth 1998). This latter 'SVL' is preferable because it can also be used on tadpoles and metamorphlings. Some authors have referred to the 'body length' of *L. raniformis* without indicating which method they used (e.g., Martin 1965; Barker and Grigg 1977; Tyler 1978, 1992; Tyler and Davies 1978; Hoser 1989; Hero *et al.* 1991).

A method for estimating the ages of wild-caught frogs of this species using skeletochronology has been developed by Ashworth (1998).

Other methods for examining eggs, tadpoles or frogs of *L. raniformis* are identical to those adopted for the closely related *L. aurea* (see Pyke & White 2001). Frogs can, for example, be weighed while suspended in small, light plastic bags from spring balances. They can be individually marked by either 'toe-clipping' (see, for example, Humphries 1979) or insertion of 'microchips' (i.e., passive integrated transponders) under the skin (see, for example, Christy 1996). Tadpoles can be captured with a small hand-net and observed in a Petri dish.

In laboratory studies some additional research techniques have been employed. Courtice (1972) anaesthetized frogs using diethyl ether, and induced females to ovulate by an injection of macerated *Bufo marinus* pituitaries. She subsequently stripped oviducal eggs from these females and used them in studies of *in vitro* fertilization. She also carried out cellulose

acetate electrophoresis using serum proteins, haemoglobin, and eye lens protein.

Captive husbandry for *L. raniformis* has been little reported. Breeding by the species under captive conditions has occurred but no details concerning methodology have been documented (Banks 1999).

Conservation and management

Litoria raniformis has been receiving increasing legislative protection, but there is scope for further protection. It is listed as 'vulnerable' under the Commonwealth *Environmental Protection and Biodiversity Conservation Act 1999* and considered 'vulnerable' in the Action Plan for Australian Frogs (Tyler 1997). It was recently added to the list of 'threatened' species on Schedule 2 of the Victorian *Flora and Fauna Guarantee Act 1988* (Mansergh *et al.* 1993; Flora and Fauna Guarantee - Scientific Advisory Committee 1999). It has also been recommended that its legal status in Tasmania be changed from 'vulnerable' to 'endangered' (Ashworth 1998). However, such legislative status requires only that likely impacts of proposed human activities on this species be considered and mitigated, if possible, before such activities are approved; they provide no explicit goals with regard to long-term survival of populations of this frog (Pyke 2000). In New Zealand *L. raniformis* is an exotic species and is not specifically protected (Pickard and Towns 1988).

Protection of the habitat of *L. raniformis* is limited as most populations of the species occur on privately-owned land, rather than in 'conservation reserves' (Ehmann and White 1997; Ashworth 1998). In Tasmania only six of the breeding populations reported by Ashworth (1998) were within conservation reserves (i.e., National Park or State Reserve). In New South Wales none of the recent records has been within a conservation reserve (Ehmann and White 1997; AMBS Consulting 2000; Pyke and Muir unpublished).

The risks of extinction for *L. raniformis* populations might be reduced through the development and implementation of pro-active strategies, as is required under various legislation. A 'Recovery Plan' for the species is required, for example, under the New South Wales Threatened Species Conservation Act 1995 and the Victorian Flora and Fauna Guarantee Act 1988 requires an 'Action Statement' for the species. However, no such plan or statement has so far been produced.

Potential strategies that could be included in a plan for recovery of *L. raniformis* are similar to those for the closely related *L. aurea* (see Pyke and White 2001). They include increased legislative protection for habitat areas occupied by the species, reduction in the impact of the Plague Minnow and other kinds of habitat modification, protection from human-induced spread of disease, translocation of individuals from one site to another (including captive breeding and release), and the development or enhancement of habitat for this frog species (Osborne 1992; Rounsevel and Swain 1993; Ayers 1995; Ashworth 1998; Bishop 2000). That this frog, like the closely-related *L. aurea*, is found in many sites that are highly disturbed by human activities, or even in some cases completely human-made, suggests that it should be possible to both develop and enhance habitat for it (Pyke and White 2001). Like *L. aurea*, this species may be adapted to a natural disturbance regime that may be replicated, either deliberately or inadvertently, by human development. None of these potential strategies for *L. raniformis* has been assessed (Osborne 1992).

Discussion

In comparison with its closely related congener the Green and Golden Bell Frog (*L. aurea*), *L. raniformis* is a relatively poorly studied species. There are presently more than 300 documents relevant to the biology of *L. aurea* (Pyke and White 2001) but only about 85 that relate to the biology of *L. raniformis* (see reference list).

Despite this lack of information concerning *L. raniformis*, it would seem that *L. raniformis* and *L. aurea* are very similar in terms of biology and conservation status. They are similar in morphology, behaviour and habitat (e.g., Courtice 1972; Courtice and Grigg 1975; Tanton 1994). They have experienced similar declines in distribution and are similarly listed as endangered, threatened or vulnerable species (see above and Pyke and White 2001). They are both waiting for the development and implementation of recovery strategies (see above and Pyke and White 2001).

Habitat development or enhancement may be important components of the recovery strategies for both *L. raniformis* and *L. aurea*. For both species, disturbance is apparently an important aspect of their habitat and both species are known to occur in sites that are largely or completely human-made. It should therefore be

possible to determine suitable disturbance regimes for these two species and duplicate them in new or modified situations. This is unlikely to be similarly possible for other frog species that require either undisturbed habitat or disturbance regimes that cannot easily be duplicated.

As is undoubtedly the case for all species of organisms, further research on *L. raniformis* is warranted. Especially relevant for this species,

however, would be investigation of patterns of habitat use, what factors control distribution and abundance, and how these factors operate. The better the understanding of habitat use, the better can be the targeted surveys for the species and any programs of habitat development or enhancement. An understanding of the factors that control distribution and abundance could lead to specific manipulations of the habitat for the benefit of this species.

Acknowledgements

This Project was supported by the Australian Museum and the Coleambally Irrigation Corporation. Margery Pyke provided invaluable assistance with obtaining copies of relevant documents. Location information was provided from databases held by the Australian Museum, NSW National Parks and Wildlife Service, Tasmanian Parks and Wildlife, Atlas of Victoria Wildlife, Museum of Victoria and South

Australian Museum. John Ashworth and Arthur White provided additional information about locations. Greg Gowing helped with computerisation and mapping of geographical data. Useful comments and suggestions were provided by Allen Greer, Liz Magarey, Angus Martin, Trent Penman, Jodi Rowley and Arthur White. For all this assistance and support I am most grateful.

References

- AMBS Consulting 2000. Biodiversity Benchmarking Survey of the Coleambally Irrigation Area. Final Report Prepared for the Coleambally Irrigation Corporation.
- Anderson, I. 1998. A great leap forward. *New Scientist* 2140, 4-5.
- Ashworth, J.M. 1998. An appraisal of the conservation status of *Litoria raniformis* (Kefferstein) in Tasmania. M.Env.Sci. Thesis, University of Tasmania, Hobart. 83 p.
- Ayers, D. 1995. *Endangered Fauna of Western New South Wales*. Published by NSW National Parks and Wildlife Service: Sydney.
- Ayers, D., Nash, S. and Baggett, K. 1996. Threatened Species of Western New South Wales. Produced as part of Western Region Biodiversity Conservation Project. NSW National Parks & Wildlife Service, Sydney, NSW.
- Banks, C. 1999. A thirty year history of Melbourne Zoo's herp department. *Herpetofauna* 29, 71-84.
- Barker, J. and Grigg, G. 1977. *A Field Guide to Australian Frogs*. Rigby, Adelaide.
- Barker, J., Grigg, G. and Tyler, M. 1995. *A Field Guide to Australian Frogs*. Surrey Beatty & Sons, Sydney, NSW.
- Bauer, A.M. and Sadler, R.A. 2000. *The Herpetofauna of New Caledonia*. Society for the Study of Amphibians and Reptiles.
- Bell, B.D. 1982a. The amphibian fauna of New Zealand. In: *New Zealand Herpetology*. NZ Wildlife Service Occasional Publication No. 2. (Ed: Newman, D.G.) N.Z. Wildlife Service, Wellington, 27-89.
- Bell, B.D. 1982b. New Zealand frogs. *Herpetofauna* 14, 1-21.
- Bennett, R. 1997. *Reptiles & Frogs of the Australian Capital Territory*. National Parks Association of the ACT Inc., Canberra. 86 pages.
- Bennett, S., Brereton, R., Mansergh, I., Berwick, S., Sandiford, K. and Wellington, C. 1991. *The potential effect of the enhanced greenhouse climate change on selected Victorian fauna*. Arthur Rylah Institute Technical Report Series No. 123. Victorian Department of Conservation and Environment, Melbourne. 224 pages.
- Berger, L. and Speare, R. 1998. Chytridiomycosis - a new disease of amphibians. *The Australian and New Zealand Council for the Care of Animals in Research and Teaching News* 11, 1-3.
- Bishop, P. 2000. Chytrid fungi identified from dying frogs in New Zealand. *Froglog* No. 39, 1-2.
- Blaustein, A.R., Hokit, D.G., O'hara, R.K., Holt, R.A. 1994. Pathological fungus contributes to amphibian losses in the Pacific Northwest. *Biological Conservation* 67, 251-254.
- Brace, E.C., Casey, B.R., Cossham, R.B., McEwan, J.M., McFarlane, B.G., Macken, J., Monro, P.A., Moreland, J.M., Northern, J.B., Street, R.J. and Yaldwyn, J.C. 1953. The frog, *Hyla aurea* as a source of animal parasites. *Tuatara* 5, 12-21.
- Brook, A.J. 1975. The distribution of Anuran amphibians in Victoria. *Victorian Naturalist* 92, 104-120.

- Brook, A.J.** 1980. The breeding seasons of frogs in Victoria and Tasmania. *Victorian Naturalist* **97**, 6-11.
- Broomhall, S.D., Osborne, W.S. and Cunningham, R.B.** 2000. Comparative effects of ambient ultraviolet-B radiation on two sympatric species of Australian frogs. *Conservation Biology* **14**, 420-427.
- Christy, M.** 1996. The efficacy of using Passive Integrated Transponder (PIT) tags without anaesthetic in free living frogs. *Australian Zoologist* **30**, 139-142.
- Clyne, D.** 1969. *Australian Frogs*. Periwinkle Books, Melbourne. 112 pages.
- Cogger, H.G.** 2000. *Reptiles & Amphibians of Australia 6th edition*. Reed Books, Sydney. 775 pages.
- Cogger, H.G., Cameron, E.E. and Cogger, H.G.** 1983. *Zoological Catalogue of Australia*. Vol. 1. *Amphibia and Reptilia*. Griffin Press, Netley, South Australia.
- Copland, S.J.** 1957. Presidential address. Australian tree frogs of the genus *Hyla*. *Proceedings of the Linnaean Society of New South Wales* **82**, 9-108.
- Copland, S.J.** 1963. Size at metamorphosis of the frog *Hyla aureus raniformis* (Keferstein). *Proceedings of the Linnaean Society of New South Wales* **88**, 105-107.
- Courtice, G.** 1972. A taxonomic revision of the *Litoria aurea* complex (Anura: Hylidae). B.Sc. (Hons) Honours Thesis, University of Sydney, Sydney. 48 p.
- Courtice, G.P. and Grigg, G.C.** 1975. A taxonomic revision of the *Litoria aurea* complex (Anura: Hylidae) in south-eastern Australia. *Australian Zoologist* **18**, 149-163.
- Cree, A.** 1984. Breeding biology, respiration, and larval development of two introduced frogs (*Litoria raniformis* and *L. ewingi*). *New Zealand Journal of Zoology* **11**, 179-188.
- Cree, A.** 1985. Water balance and nitrogen excretion of two introduced frogs (*Litoria raniformis* and *L. ewingi*). *New Zealand Journal of Zoology* **12**, 341-348.
- Cree, A.** 1988. Water balance responses of the hylid frog *Litoria aurea*. *Journal of Experimental Zoology* **247**, 119-125.
- Delvinquier, B.L.J.** 1988. On some Nyctotheridae of the Australian Anura with a description of *Nyctotheroides raffae* n. sp. *Proceedings of the Royal Society of Queensland* **99**, 21-34.
- Ehmann, H. and White, A.W.** 1997. Southern Bell Frog. In: *Threatened Frogs of New South Wales*. Habitats, Status and Conservation. (Ed. Ehmann, H.) Published by Frog and Tadpole Study Group of NSW Inc.
- Fleay, D.** 1935. Frogs devour snakes. *Victorian Naturalist* **52**, 122-123.
- Fletcher, J.J.** 1892. Contributions to a more exact knowledge of the geographical distribution of Australian batrachia. No. III. *Proceedings of the Linnaean Society of New South Wales* **7**, 7-19.
- Fletcher, J.J.** 1897. Contributions to a more exact knowledge of the geographical distribution of Australian batrachia. No. V. *Proceedings of the Linnaean Society of New South Wales* **22**, 660-688.
- Flora and Fauna Guarantee - Scientific Advisory Committee** 1999. Preliminary recommendation on a nomination for listing. *Litoria raniformis* Kerferstein 1967 - Warty Bell Frog. Prepared under Victorian Flora and Fauna Guarantee Act 1988.
- Ford, M.A.** 1983. The body and call forms of the frogs *Litoria aurea* and *Litoria raniformis* in New Zealand. M.Sc. Thesis, University of Auckland, Auckland.
- Ford, M.A.** 1986. Some observations of reproductive behaviour in captive smooth-backed green frogs (*Litoria aurea*). *Tane* **31**, 113-120.
- Gill, B.** 1986. *Collins Handguide to the Frogs and Reptiles of New Zealand*. Collins, Auckland.
- Gosner, K.L.** 1960. A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica* **16**, 183-190.
- Hero, J.-M., Littlejohn, M. and Marantelli, G.** 1991. *Frogwatch Field Guide to Victorian Frogs*. Victorian Department of Conservation and Environment, Melbourne.
- Hobbs, J.N.** 1980. Frogs as a deterrent to breeding success in reedwarblers and grassbirds. *Australian Birds* **15**, 27-29.
- Hoser, R.T.** 1989. *Australian Reptiles & Frogs*. Pierson & Co, Sydney. 235 pages.
- Horning, E.S.** 1927. Mitochondrial behaviour during the life cycle of *Nyctotherus cordiformis*. *Australian Journal of experimental Biology and medical Science* **4**, 69-73.
- Humphries, R.B.** 1979. Dynamics of a Breeding Frog Community. Ph.D. Dissertation, Australian National University, Canberra. 217 p.
- Keferstein, W.** 1867. Ueber einige neue oder seltene Batrachier aus Australien und dem tropischen Amerika. *Nachrichten von der Gesellschaft der Wissenschaften zu Göttingen* **18**:341-361.
- King, M.** 1980. C-banding studies of Australian hylid frogs: Secondary constriction structure and the concept of euchromatin transformation. *Chromosoma* **80**, 191-217.
- King, M.** 1993. A cytotaxonomic analysis of Australian hylid frogs of the genus *Litoria*. In: *Herpetology in Australia. A Diverse Discipline*. (Eds: Lunney, D.; Ayers, D.) Royal Zoological Society of NSW, Sydney, 169-175.
- Kreff, G.** 1866. On the vertebrate animals of the Lower Murray and Darling, their habits, economy, and geographical distribution. *Transactions of the Philosophical Society of New South Wales*, 1-33.

- Littlejohn, M.J.** 1963. Frogs of the Melbourne area. *Victorian Naturalist* **79**, 296-304.
- Littlejohn, M.J.** 1966. Amphibians of the Victorian mallee. *Proceedings of the Royal Society of Victoria* **79**, 597-604.
- Littlejohn, M.J.** 1967. Patterns of zoogeography and speciation in southeastern Australian amphibians. Pp. 150-174 in *Australian Inland Waters and Their Fauna*, edited by AH Weatherley. Australian National University Press: Canberra.
- Littlejohn, M.J. and Martin, A.A.** 1965. The vertebrate fauna of the bass Strait Islands:1. The amphibia of Flinders and King Islands. *Proceedings of the Royal Society of Victoria* **79**, 247-256.
- Littlejohn, M.J., Martin, A.A. and Rawlinson, P.A.** 1963. New records of frogs in East Gippsland. *Victorian Naturalist* **80**, 225-226.
- Littlejohn, M.J. and Watson, G.F.** 1993. Hybrid zones in Australian frogs: their significance for conservation. In: *Herpetology in Australia. A Diverse Discipline*. Edited by D. Lunney and D. Ayers, Royal Zoological Society of New South Wales, Sydney, 239-249.
- Loftus-Hills, J.J.** 1973. Comparative aspects of auditory function in Australian anurans. *Australian Journal of Zoology* **21**, 353-367.
- Mahony, M.** 1997. Bell frogs. Abstract for National Threatened Frog Workshop. Canberra 12-13 Nov 97.
- Mansergh, I., Davey, G. and Robertson, P.** 1993. Reptiles and amphibians of Victoria - legislation. In: *Herpetology in Australia. A Diverse Discipline*. (Eds: Lunney,D; Ayers,D) Royal Zoological Society of NSW, Sydney.
- Marriner, G.R.** 1907. On the presence of another Australian frog in New Zealand. *Transactions of the New Zealand Institute* **39**, 144-149.
- Martin, A.A.** 1965. Tadpoles of the Melbourne area. *Victorian Naturalist* **82**, 139-149.
- Martin, A.A. and Littlejohn, M.J.** 1966. The breeding biology and larval development of *Hyla jervisiensis* (Anura: Hylidae). *Proceedings of the Linnaean Society of New South Wales* **91**, 47-57.
- Martin, A.A. and Littlejohn, M.J.** 1982. *Tasmanian Amphibians*. Fauna of Tasmania handbook No. 6. University of Tasmania, Hobart.
- Martin, A.A., Littlejohn, M.J. and Rawlinson, P.A.** 1966. A key to the Anuran eggs of the Melbourne area, and an addition to the Anuran fauna. *Victorian Naturalist* **83**, 312-315.
- Maxson, L.R., Tyler, M.J. and Maxson, R.D.** 1982. Phylogenetic relationships of *Cyclorana* and the *Litoria aurea* species-group (Anura: Hylidae): A molecular perspective. *Australian Zoologist* **30**, 643-651.
- McCann, C.** 1961. The introduced frogs of New Zealand. *Tuatara* **8**, 107-120.
- Miehs, A.** 2000. Dietary patterns and prey selection in *Litoria aurea* and *Limnodynastes peronii*. B.Sc (Hons) Thesis, University of New South Wales, Sydney.
- Moore, J.A.** 1961. The frogs of eastern New South Wales. *Bulletin of the American Museum of Natural History* **121**, 149-386.
- Osborne, W.** 1990. Declining frog populations and extinctions in the Canberra region. *Bogong* **11**, 4-7.
- Osborne, W.S.** 1992. Declines and extinctions of frogs in the ACT: A discussion paper. ACT Parks and Conservation Service Internal Report 92/8.
- Parker, H.W.** 1938. The races of the Australian frog *Hyla aurea* Lesson. *Annals and Magazine of Natural History* **2(9)**, 302-305.
- Pickard, C.R. and Towns, D.R.** 1988. Atlas of the Amphibians and Reptiles of New Zealand. Conservation Sciences Publication Number 1. Science and Research Directorate, Dept of Conservation., Wellington.
- Porter, R.** 1999. The conservation of the Green and Golden Bell Frog (*Litoria aurea*) on the Central Coast of New South Wales. *Herpetofauna* **29**, 61-64.
- Pyke, G.H.** 2000. A strategy for reviewing the biology of animals. *Australian Zoologist* **31**, 482-491.
- Pyke, G.H. and Read, D.A.** 2001. Hastings River Mouse (*Pseudomys oralis*): A Biological Review. Unpublished Ms.
- Pyke, G.H. and White, A.W.** 1996. Habitat requirements for the Green and Golden Bell Frog *Litoria aurea* (Anura: Hylidae). *Australian Zoologist* **30**, 224-232.
- Pyke, G.H. and White, A.W.** 2001. A Review of the Biology of the Green and Golden Bell Frog (*Litoria aurea*). *Australian Zoologist* **31**, 563-598.
- Raff, J.W.** 1911. Protozoa parasitic in the large intestine of Australian frogs, Part 1. *Proceedings of the Royal Society of Victoria* **23**, 586-594.
- Raff, J.W.** 1912. Protozoa parasitic in the large intestine of Australian frogs, Pt. II. *Proceedings of the Royal Society of Victoria* **24**, 343-352.
- Richardson, L.R.** 1943. A case of external hernia in *Hyla aurea*. *Copeia* **1943**, 122.
- Richardson, L.R.** 1947. Second report on herniation in *Hyla aurea*. *Copeia* **4**, 255.
- Richardson, L.R.** 1952. An example of hernia in *Hyla aurea*, and its interpretation. *Transactions of the Royal Society of New Zealand* **80**, 579.
- Richardson, L.R. and Barwick, R.E.** 1957. Faulty eruption of the fore-limb in *Hyla aurea*. *Transactions of the Royal Society of New Zealand* **84**, 941-942.
- Roberts, J.D. and Maxson, L.R.** 1988. Speciation processes in southeastern Australian Anurans: A critique. *Proceedings of the Academy of Natural Science of Philadelphia* **140**, 295-307.

- Robinson, M. 1993.** A record of the warty Frog, *Litoria raniformis* feeding underwater. *Herpetofauna* 23, 39.
- Rounsevel, D. and Swain, R. 1993.** Current issues in the conservation of the terrestrial herpetofauna of Tasmania. In: *Herpetology in Australia. A Diverse Discipline*. Edited by D. Lunney and D. Ayers, Royal Zoological Society of NSW, Sydney, 71-74.
- Sadler, R.A., Pressey, R.L. and Whish, G.L. 1996.** Reptiles and Amphibians of particular conservation concern in the Western Division of New South Wales: Distributions, Habitats and Conservation Status. NSW NPWS Occasional Paper 21.
- Sherwin, W. 1978.** Narrow zones of overlap and hybridization in the genus *Litoria* (Amphibia: Anura). Unpublished Progress Report, Department of Zoology, University of Melbourne, Parkville. 58pp.
- Sherwin, W. 1995.** Pilot study of protein variations in *Litoria aurea* & *L. raniformis* in Gippsland, Victoria. Poster displayed at Green and Golden Bell Frog Conference, held on 24 May 1995 at the Australian Museum.
- Spencer, B. 1888.** Official report of Expedition to King Island by Field naturalists Club of Victoria, November 1887. *Victorian Naturalist* 4, 129-164.
- Stewart, D. 1998.** Australian Frog Calls Subtropical East. CD produced and narrated by David Stewart, Nature Sound, Mullumbimby, NSW.
- Sweet, G. 1896.** On the variations in the spinal nerves of *Hyla aurea*. *Proceedings of the Royal Society of Victoria* 9, 264-296.
- Sweet, G. 1907.** The anatomy of some Australian amphibia. A. The openings of the nephrostomes from the coelom. *Proceedings of the Royal Society of Victoria* 20, 222-238.
- Tanton, M.T. 1994.** Eden Management Area. Proposed Forestry Operations. Environmental Impact Statement. Volume B Appendix 1 - Fauna Impact Statement. Prepared for State Forests of NSW.
- Thomson, G.M. 1922.** *The naturalisation of animals and plants in New Zealand*. Cambridge University Press, Cambridge, UK. 607 pages.
- Thomson, S.A., Littlejohn, M.J., Robinson, W.A. and Osborne, W.S. 1996.** Taxonomy of the *Litoria aurea* complex: a re-evaluation of the Southern Tableland populations of the Australian Capital Territory and New South Wales. *Australian Zoologist* 30, 158-169.
- Tyler, M.J. 1978.** *Amphibians of South Australia*. D.J.Woolman, Government Printer, Adelaide. 84 pages.
- Tyler, M.J. 1979.** The impact of European man upon Australasian amphibians. Pp. ?? in *The status of endangered Australian wildlife. Proceedings of the Centenary Symposium of the Royal Zoological Society of South Australia*. (Ed: Tyler,MJ) Royal Zoological Society of South Australia, Adelaide.
- Tyler, M.J. 1982.** The hylid frog genus *Litoria* Tschudi: an overview. In: *New Zealand Herpetology*. (Ed: Newman,DG) NZ Wildlife Service, Wellington, 103-112.
- Tyler, M.J. 1992.** *Encyclopedia of Australian Animals. Frogs*. Angus & Robertson, Sydney.
- Tyler, M.J. 1997.** *The Action Plan for Australian Frogs*. Wildlife Australia, Canberra. 77 pages.
- Tyler, M.J. and Barrie, D.J. 1996.** First fossil record of the hylid frog *Litoria raniformis* (Keferstein). *Transactions of the Royal Society of South Australia* 120, 69.
- Tyler, M.J. and Davies, M. 1978.** Species-groups within the Australopapuan Hylid Frog Genus *Litoria* Tschudi. *Australian Zoologist Supplementary series No. 63*, 1-47.
- van de Mortel, T., Buttemer, W., Hoffman, P., Hays, J. and Blaustein, A. 1998.** A comparison of photolyase activity in three Australian tree frogs. *Oecologia* 115, 366-369.
- Watson, G.F. and Littlejohn, M.J. 1985.** Patterns of distribution, speciation and vicariance biogeography of southeastern Australian amphibians. Pp. 91-97 in *The Biology of Australasian Frogs and Reptiles*, edited by GC Grigg, R Shine and H Ehmann. Surrey Beatty & Sons Pty Ltd.: Sydney.
- Waite, E.R. 1928.** *The Reptiles and Amphibians of South Australia*. Harrison Weir, Government Printer, Adelaide. 270 pages.
- Wells, R.W. and Wellington, C.R. 1985.** A synopsis of the Amphibia and Reptilia of New Zealand. *Australian Journal Herpetology Supplementary Series* 1, 62-64.
- White, A.W. and Pyke, G.H. 1999.** Past distribution of *Litoria aurea* and *Litoria castanea* in the Bathurst-Orange area of New South Wales. *Herpetofauna* 29, 2-9